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The impact of hydrodynamics and hydrography on western Baltic cod early life stage survival

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Abstract:

Fish recruitment is influenced by the size and structure of the spawning stock and by variable survival of early life stages, which in turn is influenced by environmental conditions such as water temperature, salinity and oxygen conditions as well as ocean currents. The objective of this study is to assess i) the importance of different western Baltic cod spawning grounds on the early life stage survival success in relation to variability of their occurrence, ii) the impact of the timing of western Baltic cod spawning on early life stage survival, and iii) transport of western Baltic cod early life stages from spawning grounds to hatching areas. We used a spatially and temporally resolved biophysical model of the Baltic Sea in order to describe the long-term evolution of the occurrence of suitable habitats for western Baltic cod spawning. Habitat identification was based on environmental threshold levels for stage specific survival of early life stages derived from ambient hydrography. Secondly, this survival success of stage specific early life stages is described along their transport patterns obtained from biophysical modeling approaches. Generally, the long-term resolution of environmental conditions allowing western Baltic egg and yolk-sac larvae survival indicates that favorable conditions predominately occurred only in western Baltic habitats during the late spawning season in April/May, while minimum survival rates could be expected from January to March. Relative survival probability of cod eggs and yolk-sac larvae shows highest values at the end of the spawning period. Unsuitable habitats exhibiting highest mortality rates are mainly characterized by high proportions of eggs and yolk-sac larvae being lost due to the bottom contact or due to ambient water temperatures below the critical survival threshold.

Keywords: spawning habitat, egg and larval development, transport processes, environment-related western Baltic cod stage specific survival

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Introduction

The Belt Sea and the western Baltic build the transition area between the central Baltic and the Kattegat (Fig. 1). They are of fundamental importance for the water mass exchange and hence for example for the transport of biological material between both areas. The Kattegat is a shallow area with a mean depths of only 23 m, which is directly connected to the Skagerrak. In the upper layers, the water mass distribution is strongly affected by water masses of Baltic origin. The Belt Sea with its deep and narrow channels, the Great Belt and the Fehmarnbelt is on average 13 m deep. Another connection between the Kattegat and the Arkona Basin is the Sound. It consists of two sill depths east of Copenhagen with sill depths of about 8 m. A third connection between the Kattegat and the Western Baltic is the Little Belt which is situated between Jylland and the island of Fyn. Because of its only small cross section, this channel plays only a minor role for water mass exchange and transport processes between the Kattegat and the central Baltic.

The water balance of the Baltic Sea is controlled by in- and outflows through the Belt Sea, river runoff and net precipitation (Lehmann et al., 2002). Due to the freshwater surplus, in the upper layer a general outflow of brackish Baltic Sea water is forced, which is compensated by a deep inflow of saline water from the Kattegat. Dietrich (1951) was already able to relate the surface currents in the Belt Sea to the local wind conditions. Weak westerly winds (2 ms^{-1}) are necessary to stop the general outflow of brackish Baltic Sea water.

The NAO is a large-scale atmospheric pattern which has a direct influence on the climatic conditions in Europe (Hurrell, 1995; Osborn et al. 1999). Changes in the mean atmospheric circulation patterns over the North Atlantic are accompanied by pronounced shifts in storm tracks and associated eddy activity, i.e. enhanced variance over the North Atlantic and northern Europe and reduced storm track activity over the subtropical Atlantic (Hurrell and van Loon, 1997). Generally, the influence of the westerlies on the northern European climate is low under low NAO conditions (Hurrell, 1995), however, a weakened influence of the westerlies for northern Europe is a precondition of outflow for the Baltic Sea. Baltic inflows are mainly caused by persistent, i.e. of a longer-term duration, strong westerly winds over the eastern North Atlantic and northern Europe (Schinke and Matthäus, 1998). For the long-term mean, it is reasonable to assume that the volume change of the Baltic is zero, and the freshwater surplus is balanced by the outflow. Thus, the highly fluctuating in- and outflow is forced by the sea level inclination between the Kattegat and the western Baltic Sea, and is mainly responsible for the volume change on a weekly timescale (Lehmann et al., 2002).

In order to investigate potential mechanisms influencing the survival success of early life stages of Baltic cod, model scenario runs were already performed to examine the effects of the wind-driven circulation on transport processes between the western and eastern Baltic (Hinrichsen et al., 2001). A three-dimensional circulation model of the Baltic was utilized to look at relative egg and larval contribution of the western Baltic cod stock. The potential for the transport of early life stages originating from the western Baltic cod stock to drift to the eastern Baltic, and to contribute there to the juvenile population, has been recognized as being mainly due to strong westerly winds.

Management and conservation efforts can benefit from considering explicitly how environmental factors influence recruitment processes and connectivity of fish stocks. In the past, attempts have already been made to analyse how biophysical modelling can support management efforts in protecting and rebuilding fish stocks (Hinrichsen et al., 2011). Modelling activities already have analysed the causes of mortality of larval and juvenile fish by looking at the effects of advective and trophodynamic processes (e.g. Werner et al., 1996; Hinrichsen et al., 2002; Daewel et al., 2008). Subcomponents of these models were able to simulate the development of eggs and yolk-sac larvae along their drift routes in relation to physical forcing conditions, as well as growth and survival of feeding stages.

The objective of this study is to perform a long-term study to assess i) the importance of Western Baltic cod spawning grounds in relation to the variability of the spawning environment in terms of the vertical salinity distribution, ii) the transport of Western Baltic cod egg and yolk-sac larvae from the spawning to the hatching grounds and their survival success along their drift routes, and iii) the impact of transport of these life stages from the western into the eastern Baltic and subsequently the potential effects of mixing of the western and the eastern Baltic cod stocks.

Material and Methods

The applied model is a combination of a three-dimensional eddy-resolving hydrodynamic model of the Baltic Sea (Lehmann, 1995) with an Individual Based Model (IBM) considering western Baltic cod egg stages as well as the yolk-sac larval stage. This IBM tracks individuals through the aforementioned life stages. Along the drift trajectories within the coupled model, the temporal egg and yolk-sac larval development depended on ambient temperature, their survival success until the end of the yolk-sac larval stage was influenced by ambient temperature as well, but also by contact with the sea floor.

Hydrodynamic model

The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth et al., 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann et al. (2002).

The model domain comprises the entire Baltic Sea. The horizontal resolution is 5 km, with 60 vertical levels specified. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergström and Carlsson, 1994). Prognostic variables of the model are the baroclinic current field, the 3-D temperature, salinity and oxygen distributions, and the 2-D surface elevations and the barotropic transport. Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen et al., 1997; Lehmann and Hinrichsen, 2000a).

Spawning potential and drifter release locations

In the Kattegat and Øresound region, like other commercial fish species, Atlantic cod migrate towards specific sites at spawning (Fig. 1). Spatial analyses of cod landings identified several spawning areas in the Kattegat region which appeared to be most important (Vitale et al., 2008). Other major spawning grounds of western Baltic egg were described using the distribution of mature cod and the proportion of sexes as indicators (Bleil and Oeberst, 2002). The main spawning areas are the deeper regions of the Kiel Bay, Fehmarn Belt and the Mecklenburg Bay (Fig. 1). The spawning of cod in the western Baltic, the Kattegat and the Øresound takes place in late winter and spring. According to laboratory experiments (v. Westernhagen, 1970) and field observations (Westerberg, 1994), the vertical distribution of western Baltic cod eggs appears in a broad depth range. For example, in the eastern and central Baltic Sea, cod egg buoyancy varies with egg size and lipid content both of which are related to female size with large females usually producing larger more buoyant eggs (Nissling and Vallin, 1996) of higher lipid content (Graumann, 1965). The investigations performed by v. Westernhagen (1970) and Westerberg (1994) revealed variations of neutral buoyancy levels (18 to 33 psu) at which cod eggs float. This has been recently confirmed by a study in the Kiel Bay area (C. Petereit, pers. comm.). In order to consider the seasonal variability of the spawning environment in relation to its spatial and temporal variability, locations were extracted at a 5 x 5 km grid within the well known spawning areas. These locations were taken for the initial releases of the drifting particles representing newly spawned and fertilized cod eggs. In the vertical domain particles were released at 1-psu intervals, where salinities between 18 and 33 psu were available.

With respect to the temporal and vertical variability of the spawning environment a maximum spawning potential has been defined as the product of the maximum number of horizontal spawning locations ($n=339$) and the number of buoyancy levels (16; salinity between 18 and 33 psu).

Particle tracking

Simulated three-dimensional velocity fields were extracted (at a 6 hours interval) in order to develop a database for a particle tracking exercise of western Baltic cod eggs and yolk-sac larvae. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. For their whole drift periods the particles were not allowed to leave their buoyancy (density) levels at which they initially were launched. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997).

In this modelling study, we examined the drift and development of cod eggs and yolk-sac larvae released into simulated flow fields at developmental egg stage Ia. We stopped the simulations when yolk-sac larvae started to become first feeding larvae (mouth opening).

Model experiments

The main purpose of our modelling study was to analyze potential sources of variability in the spatial and temporal distribution of western Baltic cod early life stages. Since we treated eggs and yolk-sac larvae as absolutely passive drifters, i.e. they remain at the initially prescribed buoyancy levels, their final spatial distribution was exclusively determined by their survival success along the drift routes. Variability in the duration of the egg and yolk-sac larval drift

depended on variability of temperature, in this study, converted to the amount of time taken for stage Ia eggs to develop to first feeding larvae. Changes in temperature may result from several mechanisms including up- and downwelling events, advection of anomalously cold or warm water masses as well as seasonal warming and cooling. Drifters representing cod eggs were released at the forementioned release locations at 10 day intervals. In order to cover the entire spawning period of western Baltic cod, the simulations commenced on 1 December and lasted to the 30th of May. The particle tracking model was utilised for the time period 1979 to 2005 to obtain intra and inter-annual variability in distribution and transport patterns. During drift, the eggs or yolk-sac larvae were defined to die if their initially prescribed density levels were found to be higher than those obtained at positions along the drift route (i.e. hit the bottom).

Baltic Sea Index (BSI)

To obtain a general impression of how wind forcing conditions over the Baltic Sea influence mortality and survival of western Baltic cod egg and larval yolk-sac stages, we used the BSI (Hinrichsen et al., 2001; Lehmann et al., 2002), which represents the normalised sea level pressure differences Oslo (Norway) and Szczecin (Poland). The BSI is available at 3 hour intervals, but later averaged over 15 day periods, which is assumed to represent the average drift period of egg and yolk-sac larvae for the whole spawning period of western Baltic cod. Positive indices correspond to anomalous sea level pressures associated with westerly winds, whereas negative values indicate predominately easterly winds over the Baltic Sea.

Results

Spawning potential and larval survival

Generally, the resolution of 10 days spawning potentials from 1979 to 2005 that enabled egg survival just after fertilization indicate that most favorable conditions occurred during the late spawning season in April/May (Fig. 2). Minimum spawning potential could be expected from January to March, while the spawning potential for early spawners (December) was relatively high. Spatially resolved patterns were different. The spatio-temporal distribution of the spawning potential shows highest values in the Kattegat (on average > 80%), followed by the Great Belt region with a relatively high spawning potential only evident during the late spawning season. The pattern in the Øresound was similar in the late spawning period, although the spawning potential was generally lower (40 to 60%). Successful spawning in the western Baltic was highly variable and much lower compared to the aforementioned described areas.

For drifters initially released in the spawning areas of western Baltic cod, the relative survival probability of cod eggs until the end of the yolk-sac stage clearly show highest values at the end of the spawning period (Fig. 3, release events 13 to 19). While egg releases in December (release events 1 to 4) were highly variable, releases from January to the beginning of March revealed lowest survival rates. Time periods exhibiting highest mortality rates (December to February/March) are mainly characterized by high proportions of eggs being exposed to the bottom, where they die due to contact with the bottom.

The interannually averaged BSI was found to be significantly and negatively correlated to the interannually averaged survival rates of the yolk-sac larval stage. For survivors initially released as drifter in the Kattegat, the BSI explains 66%, for the Øresound 59%, the Great Belt 58%, and the western Baltic 41% of the variability. Generally, the relationships indicated that differences in sea level pressure associated with westerly winds lead to relatively low survival rates, while negative BSIs, representing easterly winds, are more beneficial for survival.

For drifters initially released as drifters in the Kattegat area, horizontal distribution maps clearly show high concentrations of bottom-related dead eggs and which mainly retained in the release area (Fig. 4). In contrast, the surviving part of the released particles destined northward of the spawning area, with particles released during the early and mid spawning season being more widely dispersed than those released during the late spawning season (Fig. 5). The dead egg fraction (only low buoyancy levels) of the Øresound spawners on average peaks in their correspondent spawning area. Similar to the Kattegat population, most of the surviving yolk-sac larvae were widely distributed over the whole Kattegat area. The non-surviving parts of the Great Belt stock component were located in close vicinity of the initial spawning area. Also the major part of the surviving fraction retained close to the spawning area, although some cohorts, mainly spawned early and in the middle of the spawning period, were advected towards the Kattegat region. The highest connectivity of the stock components was found for the most southern sub population (Kiel, Fehmarn Belt and Mecklenburg Bay). Egg mortality predominately occurred south of 55°N and only minor fractions of survivors were transported into the southern part of the Kattegat.

Discussion

In the present study, the development and survival success of western Baltic cod eggs and yolk-sac larvae which spawned within their historically important spawning grounds was investigated by detailed biophysical model simulations for the period 1979-2005. For the ecosystem under investigation, two major forcing mechanisms are predominant: vertical water mass distribution and transport of early life stages. Our model simulations analysed the influence of differences in the above mentioned forcing mechanisms and provide a baseline for quantifying and understanding corresponding variations on buoyancy levels and the final spatial distribution of early life stages originating from different spawning areas in the western Baltic Sea.

Variability in ocean circulation results in spatio-temporal differences of transport patterns of fish early life stages, which may have consequences for their survival and hence recruitment. Retention or dispersion during their development from the early egg stage Ia until the end of the yolk-sac larval stage has been identified as one of the key processes determining the survival of western Baltic cod early life stages. Generally, mortality of the eggs results from transport into areas, where buoyancy levels are not sufficient to avoid that individual eggs will die due to contact with the bottom. In order to correctly predict egg and larval survival success based on transport processes, a relatively high level of complexity in initial conditions is required (Gallego et al., 2007). Thus, for a model that predicts spatial and temporal patterns in absolute numbers of surviving eggs and larvae, for example input in the form of spatially and temporally resolved egg production is needed (Heath and Gallego, 1998). Unfortunately,

this is not the case for western Baltic cod, thus with our investigations we only were able to analyse relative survival rates.

In the western Baltic Sea, the highly dynamic hydrographic conditions provide a complex environmental scenario which limits the survival success of cod early life stages, and where the effects of age structure and female condition might also have a non-negligible impact on the dynamic of the cod stock (e.g. Nissling and Vallin, 1996). The spawning potential and timing determine the drift of eggs and yolk-sac larvae, which leads to the conclusion that spawning date and location in conjunction with climatic conditions determine early life stage drift duration, destination and survival. Furthermore, this study indicated the importance of timing of cod spawning associated with high sea level pressure (low BSI) over the Baltic Sea for the survival success of yolk-sac larvae. Drift patterns and yolk-sac larval success differed over the spawning season. Lower ambient temperatures and the correspondingly longer developmental times of eggs and yolk-sac larvae during the early and in the middle of the spawning season were associated with longer drift durations, larger drift distances and a relatively small fraction of survivors remaining in their spawning areas. During the early spawning period when the probability of survival was extremely low most of the eggs tended to be transported to coastal environments or to the eastern Baltic. Generally, at the end of the spawning period survival rates are relatively high which is i) slightly associated with higher ambient temperatures (shorter drift duration and distances) and is ii) mainly associated with wind-induced westerly particle transport. The latter avoids eggs to be transported into regions of low buoyancy such as in the eastern Baltic.

Bleil and Oeberst (1997) separated cod juveniles caught during trawl surveys in the more eastern Baltic (Arkona and Bornholm Basin) into origins from the western and eastern stock, based on their different total lengths as well as on their different spawning dates derived from otolith age readings (Hinrichsen et al. 2001). There were several different reasons taken into account why juveniles of the two different stocks were found in the eastern Baltic Sea. First, but presently nonverified, adult cod of the western stock in spawning condition migrated actively eastwards and their offsprings remained in these nursery areas for longer: This is not very likely as during trawl fishery carried out between February and April never cod in spawning condition was caught in the eastern Baltic Sea (Bleil and Oeberst, 1997). Secondly, eastward directed water mass transport suggested the probability of an advective exchange of early life stages of the western stock towards the deep eastern basins of the Baltic Sea (Hinrichsen et al., 2001). However, the present study limits the possibility of an advective exchange between the western and eastern Baltic stocks only to feeding larvae and/or juveniles, because the majority of eggs and yolk-sac larvae being exposed to the bottom and thus experience lethal conditions before entering the eastern Baltic Sea. Because of the on average lower salinity range predominant in the western Baltic (11 to 18 psu), absolutely passively drifting particles such as cod eggs and larvae will not meet the required environmental condition for survival.

To our knowledge, this study is the first one to provide potential evidence for temporal and spatial differences of the reproduction probability and the yolk-sac larval survival success of the western Baltic cod stock based on biophysical modeling activities. Without taking into account data and detailed knowledge on the reproduction biology of western Baltic cod, this approach seems to be able to provide a guideline for the spatial distributions and temporal windows of high yolk-sac larval survival, which could be used to objectively define particle release areas, which in our case would represent larvae at the transition from endo- to

exogenous feeding. Usually, processes operating at relatively small scales are normally poorly resolved. Many of the conclusions about the physical environmental conditions in the Baltic Sea mainly depend on long-term time series data analyses which are not able to resolve environment-dependent processes on smaller temporal and spatial scales. Hence, this approach appears to be able to more effectively support fisheries stock assessment by condensing, summarizing and visualizing the highly resolved information obtained from the biophysical model to scales presently used in fisheries management models (Gallego et al., 2007). In future, approaches that combine observations, process knowledge, and numerical modelling, might be a promising tool in simulating the dynamics of the western Baltic cod stock. Despite of the lack of necessary information on e.g. stock demography, egg production rates, etc., this application of a biophysical model can be seen as an direct attempt to characterize the spatial and temporal variability of western Baltic cod spawning habitat and subsequent survival success of early life stages in the light of implementing closed areas or seasons to ensure undisturbed spawning. Furthermore, our case study exemplifies the effects of climate variability for the understanding of the dynamics of fish stocks. Hence, long-term fisheries management has to consider climate forcing on recruitment in order to achieve optimal resource utilization and conservation (Köster et al., 2005).

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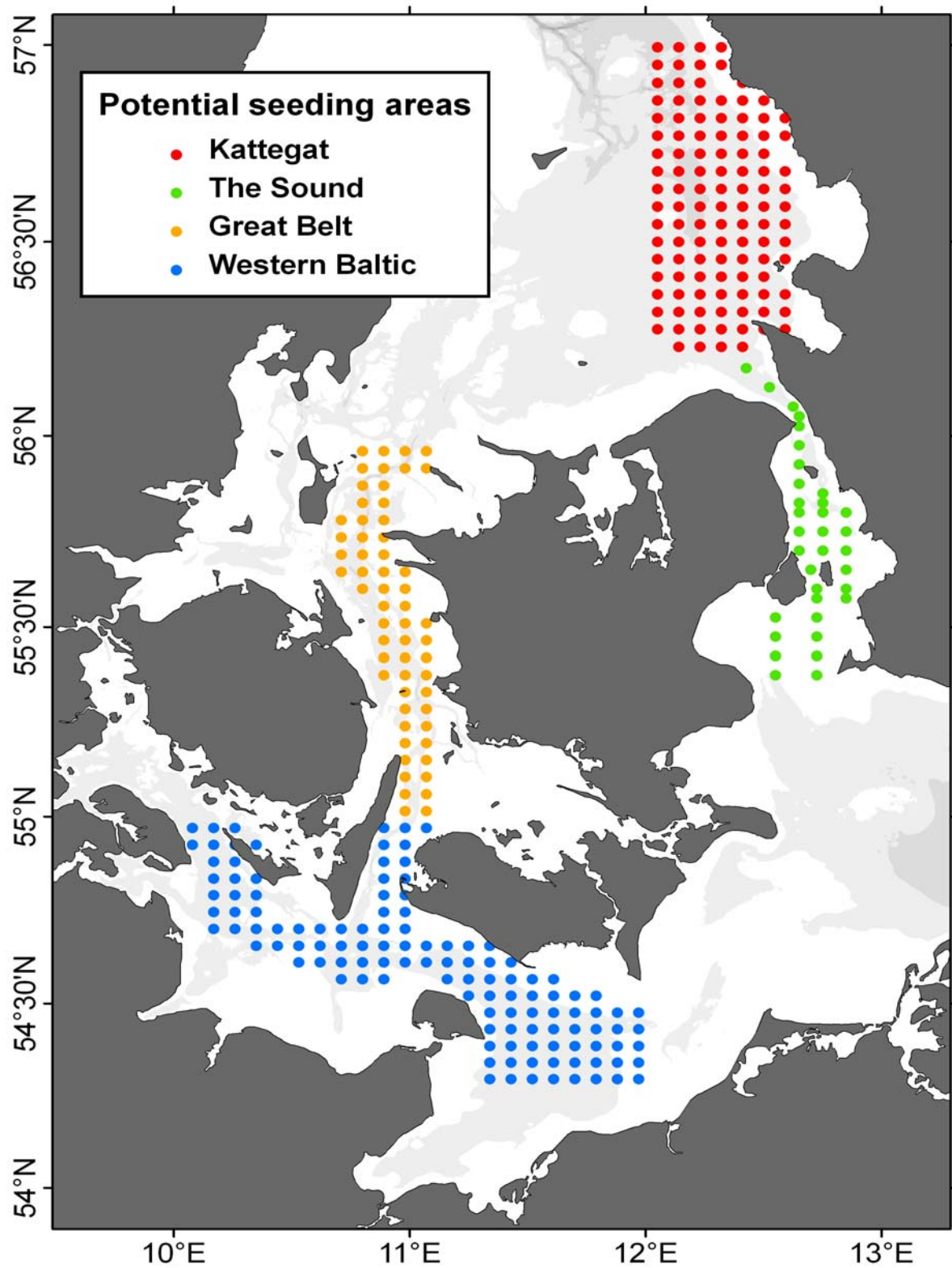


Figure 1: The western Baltic and spawning areas of the western Baltic cod stock. Spawning areas were used as seeding areas for drift experiments

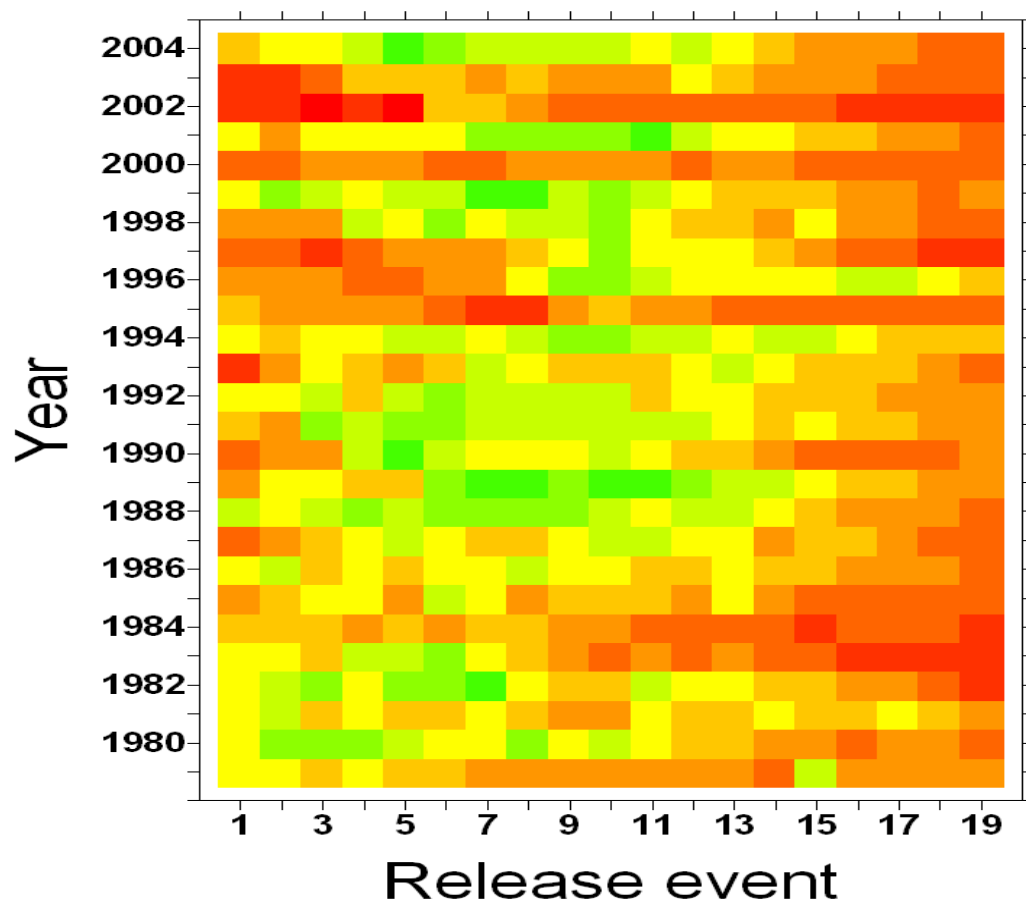


Figure 2: Reproduction potential as numbers of eggs released in all spawning areas for salinity classes between 18 and 33 psu

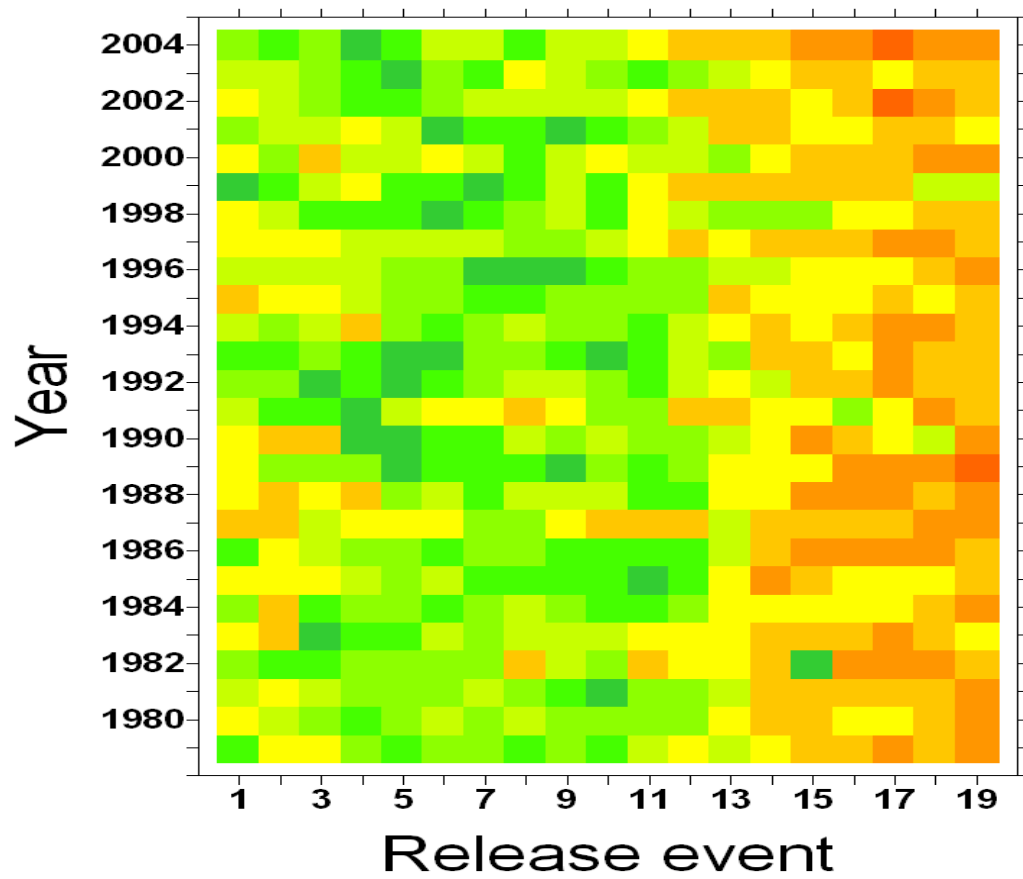


Fig. 3: Yolk-sac larval survival probabiliy for eggs initially released in all spawning areas

Dead eggs

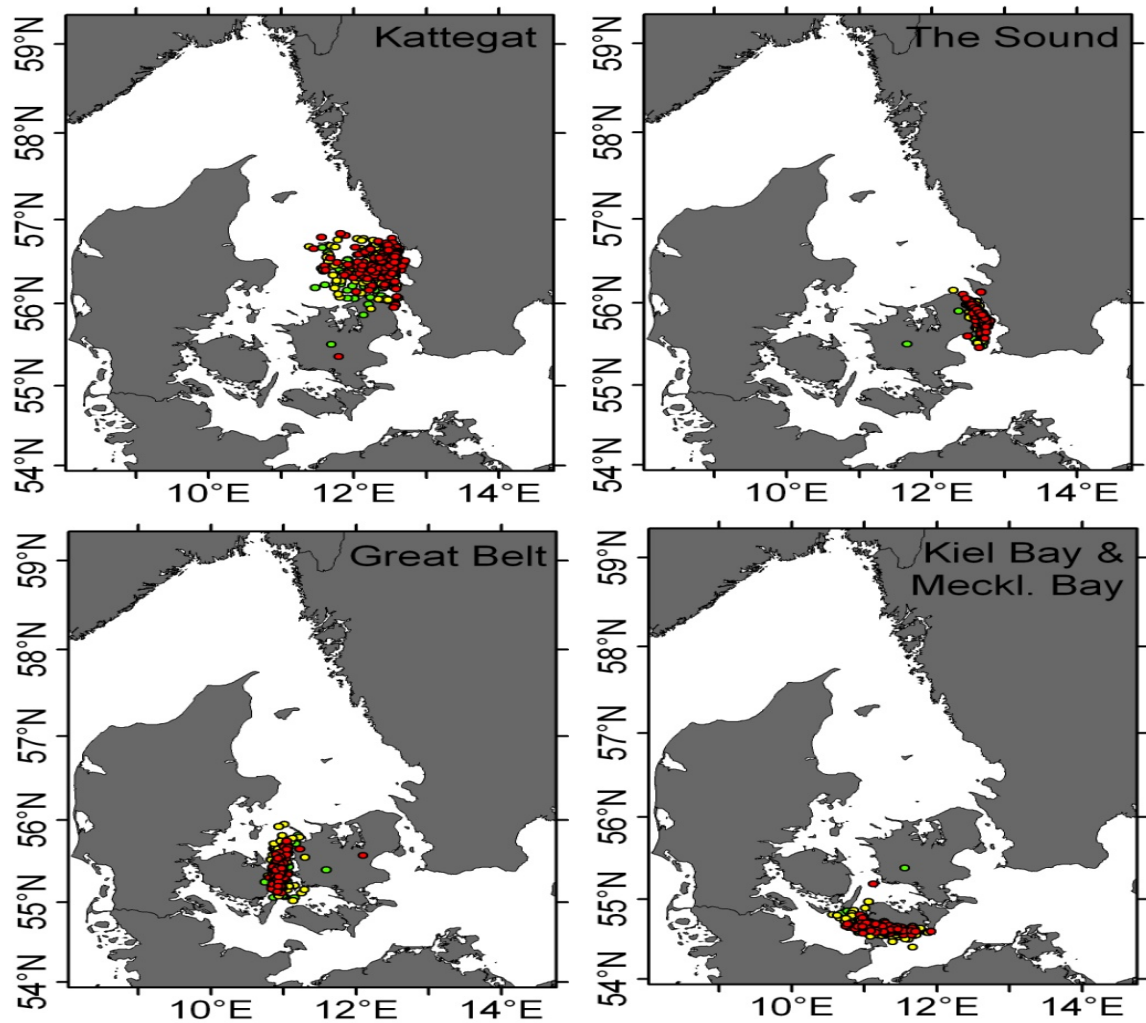


Fig. 4: Mean locations of dead eggs for cohorts initially released in the western Baltic during the spawning periods 1979-2005 (green – early, yellow – middle, red - late spawning period)

Surviving yolk-sac larvae

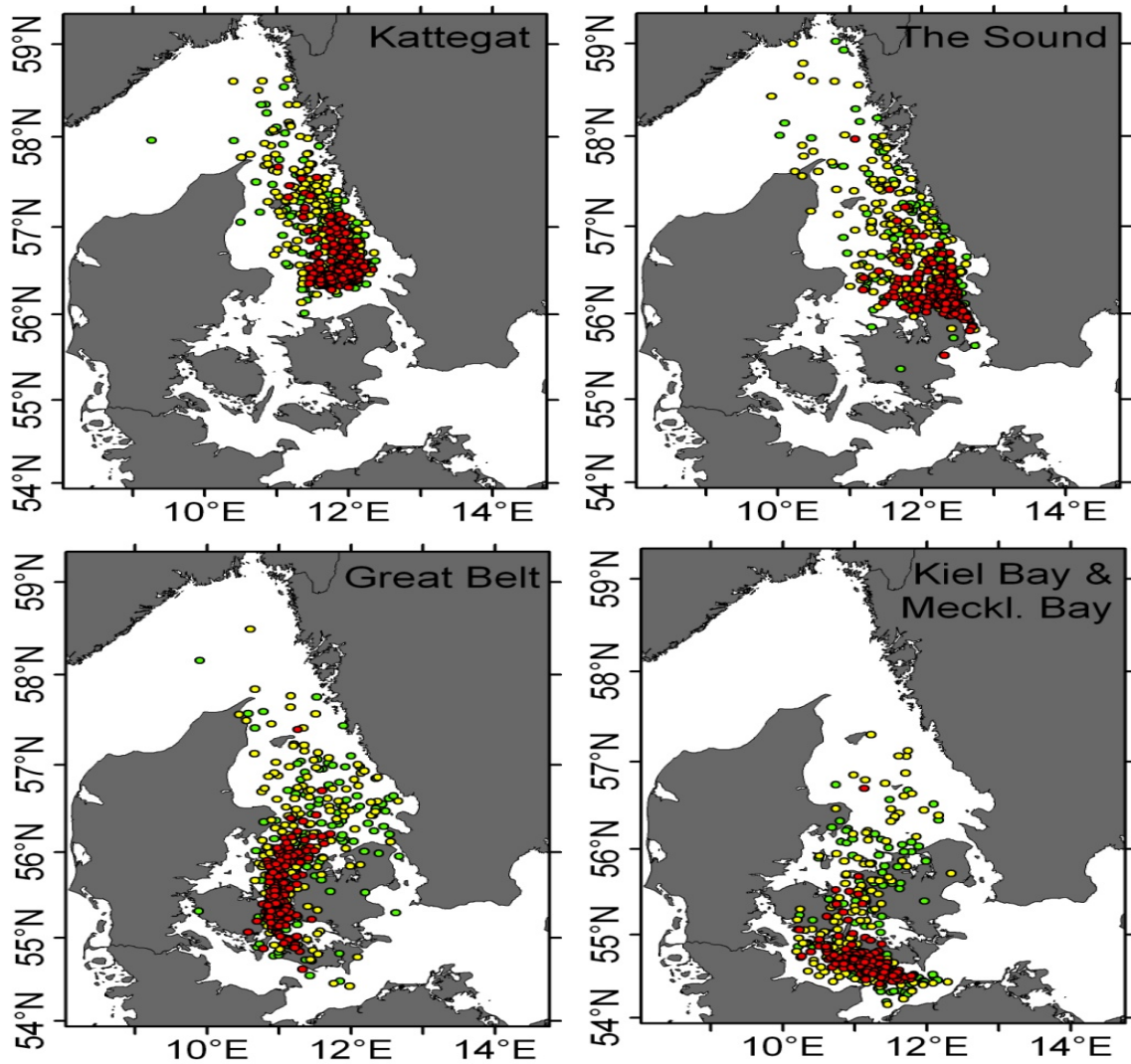


Fig. 5: Mean locations of survived yolk-sac larvae for cohorts initially released in the western Baltic during the spawning periods 1979-2005 (green – early, yellow – middle, red - late spawning period)